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## ABSORPTION OF NUTRIENTS AS AFFECTED BY THE NUMBER OF ROOTS SUPPLIED WITH THE NUTRIENT

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### INTRODUCTION

In the course of several investigations on the mineral nutrition of rice (*Oryza sativa*) it became necessary to know whether the plant could absorb an optimum amount of the mineral element which was supplied to only part of the roots if all the other essential elements were supplied to all the roots. At first thought it would seem the plant could absorb sufficient of the element supplied to only part of its roots if sufficient selection could be exercised in the absorption of the different nutrients by individual roots. So far as known, no quantitative study has been made of this point; hence, the tests reported below were conducted.

The selective absorption of mineral elements was early established by Saussure,<sup>1</sup> Gorup-Besanez,<sup>1</sup> and W. Wolf (12).<sup>2</sup> E. Wolff (13) showed that the selective absorption could be altered by changing the proportion of salts in the nutrient solution. Some recent studies on antagonism have also demonstrated that absorption or penetration of ions in plant roots is affected by the relative concentrations of ions in the solution. Most of such studies, however, have been made on unbalanced solutions of one or two salts only, and the object has been to ascertain the influence of different proportions of salts on root growth aside from nutritive effects. The results show that a nutrient solution, to be a proper medium for root growth, must contain the salts in certain proportions. These proportions may be varied considerably, especially in low concentrations of a variety of salts, without appreciably affecting growth (3, 11).

The present work does not deal with the effect of the medium on selective absorption by roots, but with the effect of localization of the supply. The results emphasize to what a great extent selective absorption may be altered by limiting the supply of an element to a few roots, without changing the medium. Some work done previously is similar to this investigation, in that plants were grown with their roots divided between two unlike media. Quantitative data, however, were not secured on the point which is the subject of this work.

<sup>1</sup> Cited by Heiden (6, p. 286-287). <sup>2</sup> Reference is made by number to "Literature cited," p. 94-95.

Frank (2, p. 153) grew corn and peas with roots divided between two compartments, one of which contained calcium nitrate and the other of which did not. The only result reported was that roots in the compartment with nitrate made a much more luxuriant development of side roots. He describes the experiment as being similar to one of Müller-Thurgau's. Nobbe (9), growing corn in pots with fertilizer applied to different parts of the soil, also observed that the development of lateral roots was much greater in those zones where fertilizers had been applied.

Faack (1) grew wheat with part of the roots in a solution lacking one element and a few roots in a solution containing the single salt not present in the main solution. He found that the plant would grow without marked disturbance under these conditions if the proper salt and proper concentration were used in the single salt solution. As only two plants per lot were used, his data do not show the extent to which growth and absorption were affected.

#### METHOD OF EXPERIMENTS

The experiments were carried out in water cultures, as it is obviously difficult to maintain a good separation of roots and localize the distribution of salts in sand cultures. Erlenmeyer flasks of "Nonsol" or Jena glass joined together at the necks were used as receptacles. The plants were grown with their roots divided between the two flasks, one of which contained a complete nutrient solution and the other a nutrient solution lacking one element.

Rice seedlings were germinated over distilled water for Experiments I, III, and IV, but in tap water for subsequent experiments, as root development was better in tap water and there was no need of excluding all mineral salts before starting the experiment. Corn (*Zea mays*) was germinated in sphagnum moss. One corn seedling or two rice seedlings were grown in each double flask.

The compositions of the nutrient solutions used are shown in Table I.

TABLE I.—Composition of nutrient solutions used

| Solution.   | Complete acid solution. | Complete neutral solution. | Nitrogen-free solution. | Phosphorus-free solution. | Potassium-free solution. |
|---|-------------------------|----------------------------|-------------------------|---------------------------|--------------------------|
|   | Gm.                     | Gm.                        | Gm.                     | Gm.                       | Gm.                      |
| Potassium nitrate ( $\text{KNO}_3$ ).....                                     | 10.71                   | 10.71                      | .....                   | 10.71                     | .....                    |
| Monopotassium phosphate ( $\text{KH}_2\text{PO}_4$ ).....                     | 7.14                    | 3.57                       | 3.57                    | .....                     | .....                    |
| Dipotassium phosphate ( $\text{K}_2\text{HPO}_4$ ).....                       | .....                   | 3.57                       | 3.57                    | .....                     | .....                    |
| Monosodium phosphate ( $\text{NaH}_2\text{PO}_4$ ).....                       | .....                   | .....                      | .....                   | .....                     | 6.30                     |
| Sodium nitrate ( $\text{NaNO}_3$ ).....                                       | 21.43                   | 21.43                      | .....                   | 21.43                     | 14.30                    |
| Sodium sulphate ( $\text{Na}_2\text{SO}_4 \cdot 10\text{H}_2\text{O}$ ).....  | 3.15                    | 3.15                       | 3.15                    | .....                     | 3.15                     |
| Calcium chloride ( $\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$ ).....           | 2.00                    | 2.00                       | 37.60                   | 2.00                      | .....                    |
| Magnesium chloride ( $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$ ).....         | 2.00                    | 2.00                       | 35.60                   | 2.00                      | 2.00                     |
| Potassium sulphate ( $\text{K}_2\text{SO}_4$ ).....                           | .....                   | .....                      | 12.40                   | 6.20                      | .....                    |
| Calcium nitrate ( $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ )..... | .....                   | .....                      | .....                   | .....                     | 21.86                    |
| Iron (Fe).....  | .80                     | .80                        | .80                     | .80                       | .80                      |
| Sulphuric acid ( $\text{H}_2\text{SO}_4$ ).....                               | .25                     | .....                      | .....                   | .....                     | .25                      |
| Distilled water.....  | 100,000 c. c.           |                            |                         |                           |                          |

The form in which the iron was added varied in some experiments, although it was used at the rate of 0.8 gm. of iron per 100,000 c. c. in all experiments except IX. The iron-free solution was the same as the complete solution, except for the absence of iron. Water used in the nutrient solutions was distilled from a cast-iron still with tin condenser and stored in a tin-lined copper tank.

The solutions were generally changed every four days, except that, when the plants were first inserted, they were left for six days. Sometimes when growth was especially rapid, as with corn, the solutions were renewed more frequently. Transpired water was made up with distilled water every day. In all the experiments rice was grown for 40 days and corn for 21 days.

In analyzing the plants the usual analytical methods were used, except that iron was determined by the colorimetric method with sulphocyanic acid (HSCN) (10).

#### EXPERIMENTAL RESULTS

##### EXPERIMENT I.—RICE WITH HALF THE ROOTS IN A NITROGEN-FREE SOLUTION

In this test the complete neutral and nitrogen-free solutions shown in Table I were used, with ferrous sulphate as the source of iron. In one lot half the roots were maintained in the complete and half in the nitrogen-free solution. In other lots all the roots were kept either in the complete solution or in the nitrogen-free solution. The plants without nitrogen were grown in 200-c. c. flasks for 40 days; all others in 200-c. c. flasks for 22 days, and in 500-c. c. flasks for 18 days. Six double flasks were taken as a unit and the units triplicated for each treatment. Solutions were changed seven times in the course of the experiment. Experimental data are given in Tables II and III.

TABLE II.—Growth of rice in Experiment I

| Nutrient solution. |                    | Weight of stalks and leaves. |                          |                         | Number of roots.  |                   | Average oven-dry weight of roots. |           | Ratio of roots to tops. |           |
|--------------------|--------------------|------------------------------|--------------------------|-------------------------|-------------------|-------------------|-----------------------------------|-----------|-------------------------|-----------|
| A-flasks.          | B-flasks.          | Flask No.                    | Green.                   | Oven-dry.               | Average oven-dry. | A-flasks.         | B-flasks.                         | A-flasks. |                         | B-flasks. |
|                    |                    |                              |                          |                         |                   |                   |                                   |           |                         |           |
| Nitrogen-free..... | Nitrogen-free..... | 1-6<br>7-12<br>13-18         | Gm. 1.59<br>1.62<br>1.71 | Gm. 0.43<br>.41<br>.47  | Gm. 0.42          | 49<br>44<br>41    | 51<br>47<br>58                    | Gm. 0.119 | Gm. 0.144               | 0.606     |
| Do.....            | Complete.....      | 19-24<br>25-30<br>31-36      | 75.40<br>80.53<br>73.54  | 11.73<br>11.88<br>10.25 | 21.29             | 195<br>231<br>189 | 195<br>185<br>190                 | 2.271     | 2.274                   | .403      |
| Complete.....      | do.....            | 37-43<br>43-48<br>49-54      | 96.77<br>90.44<br>85.13  | 13.13<br>13.34<br>12.36 | 12.93             | 215<br>225<br>390 | 193<br>194<br>204                 | 2.198     | 2.044                   | .348      |

TABLE III.—Nitrogen and phosphoric acid absorbed by rice in Experiment I

| Flask No. | Nitrogen (N) in dry stalks and leaves. | Nitrogen (N) in dry roots. |           | Nitrogen (N) absorbed by 12 plants. | Nitrogen (N) absorbed per gram of roots. | Phosphoric acid (P <sub>2</sub> O <sub>5</sub> ) in dry stalks and leaves. |
|-----------|--|----------------------------|-----------|-------------------------------------|--|--|
|           |  | A-flasks.                  | B-flasks. |                                     |  |  |
|           | Per cent.                              | Per cent.                  | Per cent. | Gm.                                 | Gm.                                      | Per cent.  |
| 1-18      | 1.32                                   | 0.97                       | 0.97      | .....                               | .....                                    | .....  |
| 19-36     | 3.90                                   | 1.47                       | 2.12      | 0.5138                              | 0.226                                    | 1.61   |
| 49-54     | 4.40                                   | 2.41                       | 2.41      | .6631                               | .156                                     | 1.54   |

If the plants with all their roots in the complete solution are considered as normal in growth and nitrogen content, it is evident that the plants partially supplied with nitrogen made slightly less than normal growth, had 23 per cent greater ratio of roots to tops,<sup>1</sup> and absorbed 0.77 of the normal amount of nitrogen. The influence of the need of the plant on the selective absorption of nitrogen is shown by the amount of nitrogen absorbed per gram of roots, the partial-nitrogen plants having absorbed 1.45 times as much nitrogen as the normal plants.

#### EXPERIMENT II.—CORN WITH HALF THE ROOTS IN NITROGEN-FREE SOLUTION

It was thought desirable to repeat the preceding test with corn, so that the results might not be taken as being peculiar to rice alone. Because of the rapid growth, corn could be grown for 21 days only instead of 40, with the means at our disposal.

No-nitrogen plants were grown in 200-c. c. flasks for the 21 days; all others in 200-c. c. flasks for 11 days, 500-c. c. flasks for 4 days, and 1,000-c. c. flasks for 6 days. The nutrient solutions used were the same as in Experiment I, and were changed six times during the experiment. Eight flasks were taken as a unit and the units duplicated for each treatment. Experimental data are given in Tables IV and V.

TABLE IV.—Growth of corn in Experiment II

| Nutrient solution. |                    | Flask No.                     | Weight of stalks and leaves. |                             |                               | Number of roots.     |                      | Average oven-dry weight of roots. |                     | Ratio of roots to tops. |
|--------------------|--------------------|-------------------------------|------------------------------|-----------------------------|-------------------------------|----------------------|----------------------|-----------------------------------|---------------------|-------------------------|
| A-flasks.          | B-flasks.          |                               | Green.                       | Oven-dry.                   | Average oven-dry.             | A-flasks.            | B-flasks.            | A-flasks.                         | B-flasks.           |                         |
| Nitrogen-free..... | Nitrogen-free..... | 1-8<br>9-16<br>17-24<br>25-32 | Gm.<br>12.4<br>15.2<br>15.0  | Gm.<br>1.55<br>1.77<br>1.78 | Gm.<br>1.91<br>2.27<br>1.5-25 | 37<br>38<br>67<br>69 | 45<br>37<br>74<br>62 | Gm.<br>0.80<br>2.51               | Gm.<br>0.71<br>1.94 | 0.791<br>0.226          |
| Do.....            | Complete.....      | 33-40<br>41-48                | 270.0<br>255.0               | 21.93<br>19.36              | 20.59                         | 77<br>78             | 87<br>84             | 1.87                              | 1.92                | 1.184                   |

<sup>1</sup> The ratio of roots to tops is taken as the weight of dry roots divided by the weight of dry stalks and leaves.

TABLE V.—Nitrogen and phosphoric acid absorbed by corn in Experiment II

| Flask No. | Nitrogen (N) in dry stalks and leaves. | Nitrogen (N) in dry roots. |           | Nitrogen (N) absorbed per 8 plants. | Nitrogen (N) absorbed per gram of roots. | Phosphoric acid (P <sub>2</sub> O <sub>5</sub> ) in dry stalks and leaves. |
|-----------|--|----------------------------|-----------|-------------------------------------|--|--|
|           |  | A-flasks.                  | B-flasks. |                                     |  |  |
|           | Per cent.                              | Per cent.                  | Per cent. | Gm.                                 | Gm.                                      | Per cent.  |
| 1-16      | 1.00                                   | 0.79                       | 0.79      | .....                               | .....                                    | 1.80   |
| 17-32     | 3.66                                   | 1.48                       | 2.72      | 0.6023                              | 0.310                                    | 1.28   |
| 33-48     | 3.57                                   | 2.46                       | 2.46      | .7973                               | .210                                     | 1.26   |

The partial-nitrogen plants made noticeably less growth than the normal plants, had 23 per cent greater ratio of roots to tops, absorbed 0.76 of the normal amount of nitrogen, and absorbed 1.48 times as much nitrogen per gram of roots as the normal plants. These figures agree remarkably well with those obtained in the previous experiment with rice.

EXPERIMENT III.—RICE WITH HALF THE ROOTS IN NITROGEN-FREE SOLUTION

EFFECT OF INCREASING CONCENTRATION OF NITROGEN

A test was conducted comparing the ordinary neutral solution with one containing twice the amount of nitrogen, to make sure the previous results were not influenced by a scarcity of nitrogen and to observe the effect on absorption of increasing the nitrogen.

The double-nitrogen solution was the same as the complete solution, except that the quantities of both potassium nitrate and sodium nitrate were doubled. Ferric citrate was used as the source of iron. The plants without nitrogen were grown in 200-c. c. flasks for 40 days; all others were grown in 200-c. c. flasks for 18 days, and in 500-c. c. flasks for the last 22 days. Eight flasks were taken as a unit and the units duplicated for each treatment. The solutions were changed eight times during the experiment. Experimental data are given in Tables VI and VII.

TABLE VI.—Growth of rice in Experiment III

| Nutrient solution.        |                           | Flask No. | Weight of stalks and leaves. |           |                   | Number of roots. |           | Average oven-dry weight of roots. |           | Ratio of roots to tops. |
|---------------------------|---------------------------|-----------|------------------------------|-----------|-------------------|------------------|-----------|-----------------------------------|-----------|-------------------------|
| A-flasks.                 | B-flasks.                 |           | Green.                       | Oven-dry. | Average oven-dry. | A-flasks.        | B-flasks. | A-flasks.                         | B-flasks. |                         |
| Nitrogen-free             |                           |           | Gm.                          | Gm.       | Gm.               |                  |           | Gm.                               | Gm.       |                         |
| Do                        | Nitrogen-free             | 1-8       | 1.62                         | 0.45      | 0.47              | 51               | 33        | 0.14                              | 0.12      | 0.55                    |
|                           |                           | 9-16      | 2.77                         | .49       |                   | 50               | 44        |                                   |           |                         |
| Do                        | Complete                  | 17-24     | 61.33                        | 12.53     | 12.60             | 205              | 227       | 3.69                              | 2.00      | .793                    |
|                           |                           | 25-32     | 89.99                        | 13.57     |                   | 230              | 225       |                                   |           |                         |
| Do                        | Complete double nitrogen. | 33-40     | 93.25                        | 13.40     | 12.69             | 209              | 213       | 3.60                              | 1.86      | .723                    |
|                           |                           | 41-48     | 93.39                        | 12.98     |                   | 210              | 204       |                                   |           |                         |
| Complete                  | Complete                  | 49-56     | 114.89                       | 15.18     | 16.39             | 247              | 237       | 2.09                              | 1.84      | .747                    |
|                           |                           | 57-64     | 129.95                       | 17.45     |                   | 259              | 245       |                                   |           |                         |
| Complete double nitrogen. | Complete double nitrogen. | 65-72     | 145.35                       | 19.54     | 18.00             | 250              | 274       | 2.75                              | 2.13      | .743                    |
|                           |                           | 73-80     | 137.47                       | 16.45     |                   | 266              | 267       |                                   |           |                         |

TABLE VII.—Nitrogen and phosphoric acid absorbed by rice in Experiment III

| Flask No. | Nitrogen (N) in dry stalks and leaves. | Nitrogen (N) in dry roots. |           | Nitrogen (N) absorbed by 16 plants. | Nitrogen (N) absorbed per gram of roots. | Phosphoric acid (P <sub>2</sub> O <sub>5</sub> ) in dry stalks and leaves. |
|-----------|--|----------------------------|-----------|-------------------------------------|--|--|
|           |  | A-flasks.                  | B-flasks. |                                     |  |  |
|           | Per cent.                              | Per cent.                  | Per cent. | Gm.                                 | Gm.                                      | Per cent.  |
| 1-16      | 1.03                                   | 0.93                       | 0.93      | .....                               | .....                                    | .....  |
| 17-32     | 4.35                                   | 1.38                       | 2.41      | 0.6124                              | 0.306                                    | 1.50   |
| 33-48     | 4.49                                   | 1.47                       | 2.60      | .6344                               | .341                                     | 1.55   |
| 49-64     | 4.55                                   | 2.35                       | 2.35      | .8277                               | .211                                     | 1.63   |
| 65-80     | 4.52                                   | 2.35                       | 2.35      | .9093                               | .208                                     | 1.60   |

A comparison of plants 49 to 64 with 65 to 80 shows that, when all the roots of the plants were in the complete solution, doubling the nitrogen in the solution had no effect on the ratio of roots to tops, the nitrogen content of the plants, nor the amount of nitrogen absorbed per gram of roots. The slight increase in the weight of tops for 65 to 80 and the consequent increase in the total amount of nitrogen absorbed is of doubtful significance, as this increase is no greater than the variation between duplicates of the same lot.

A comparison of plants 17 to 32 with 33 to 48 shows that doubling the nitrogen in the solution, when the plants had only half their roots in the solution, had no effect on the growth of tops, but lowered the ratio of roots to tops, very slightly increased the total amount of nitrogen absorbed, and noticeably increased the amount of nitrogen absorbed per gram of roots. It is evident from these comparisons that, with the ordinary complete solution, the absolute amount of nitrogen supplied was sufficient for all the plants, and the previous results obtained were not due to a scarcity of nitrogen.

It follows from the preceding comparisons that doubling the nitrogen in the solution did not enable the partial-nitrogen plants to approach appreciably nearer the maximum nitrogen absorption (the amount of nitrogen absorbed by plants with all roots in the complete solution), although it did enable them to absorb more nitrogen per gram of roots. These facts are more evident from the following calculations: Plants 17 to 32 absorbed 0.74 as much nitrogen as 49 to 64, had 22 per cent greater ratio of roots to tops, and absorbed 1.45 times as much nitrogen per gram of roots, while plants 33 to 48 absorbed 0.77 as much nitrogen as 49 to 64, had 13 per cent greater ratio of roots to tops, and absorbed 1.62 times as much nitrogen per gram of roots.

#### EXPERIMENT IV.—RICE WITH THREE-FOURTHS THE ROOTS IN NITROGEN-FREE SOLUTION

It was important to see whether the rate at which the roots absorbed nitrogen could be still further increased by decreasing the number of roots in the complete nutrient solution. Accordingly in this experiment one lot of plants was grown with approximately three-fourths of its

roots in the nitrogen-free solution and one-fourth in the complete solution.

The nutrient solutions used were the same as those in Experiments I and II. The no-nitrogen plants were grown 30 days in 200-c. c. flasks; all others, 27 days in 200-c. c. flasks and 13 days in 500-c. c. flasks. Six flasks were taken as a unit and the units triplicated for each treatment. Solutions were changed eight times during the experiment. Experimental data are given in Tables VIII and IX.

TABLE VIII.—Growth of rice in Experiment IV

| Nutrient solution. |           | Flask No. | Weight of stalks and leaves. |           |                   | Number of roots. |           | Average oven-dry weight of roots. |           | Ratio of roots to tops. |
|--------------------|-----------|-----------|------------------------------|-----------|-------------------|------------------|-----------|-----------------------------------|-----------|-------------------------|
| A-flasks.          | B-flasks. |           | Green.                       | Oven-dry. | Average oven-dry. | A-flasks.        | B-flasks. | A-flasks.                         | B-flasks. |                         |
| Nitrogen free..... |           | 1-6       | 1.50                         | 0.36      |                   | 54               | 55        |                                   |           |                         |
|                    |           | 7-12      | 1.47                         | .37       | 0.37              | 44               | 45        |                                   |           |                         |
|                    |           | 13-18     | 1.49                         | .38       |                   | 45               | 46        | 0.145                             | 0.147     | 0.797                   |
|                    |           | 19-24     | 53.11                        | 8.44      |                   | 247              | 75        |                                   |           |                         |
| Do.....            |           | 25-30     | 47.15                        | 7.03      | 8.30              | 191              | 80        | 2.732                             | 1.025     | .453                    |
|                    |           | 31-36     | 53.92                        | 8.53      |                   | 259              | 72        |                                   |           |                         |
|                    |           | 37-42     | 85.50                        | 12.27     |                   | 212              | 157       |                                   |           |                         |
| Complete.....      |           | 43-48     | 84.83                        | 11.41     | 12.41             | 198              | 207       | 2.103                             | 2.732     | .341                    |
|                    |           | 49-54     | 85.66                        | 12.55     |                   | 188              | 212       |                                   |           |                         |

TABLE IX.—Nitrogen and phosphoric acid absorbed by rice in Experiment IV

| Flask No. | Nitrogen (N) in dry stalks and leaves. | Nitrogen (N) in dry roots. |           | Nitrogen (N) absorbed by 12 plants | Nitrogen (N) absorbed per gram of roots. | Phosphoric acid (P <sub>2</sub> O <sub>5</sub> ) in dry stalks and leaves. |
|-----------|--|----------------------------|-----------|------------------------------------|--|--|
|           |  | A-flasks                   | B-flasks  |                                    |  |  |
|           | Per cent.                              | Per cent.                  | Per cent. | Gm.                                | Gm.                                      | Per cent.  |
| 1-18      | 1.33                                   | 0.50                       | 0.50      |                                    |  |  |
| 19-36     | 3.72                                   | 1.37                       | 2.38      | 0.3642                             | 0.355                                    | 1.60   |
| 37-54     | 4.63                                   | 2.47                       | 2.47      | .6666                              | .157                                     | 1.60   |

If we assume that plants 37 to 54 were normal in growth and composition, it appears that plants 19 to 36, with one-fourth of their roots in the complete solution, made about two-thirds the normal growth, had a 33 per cent higher ratio of roots to tops, absorbed 0.55 of the normal amount of nitrogen, and, per gram of roots, absorbed 2.26 times the normal amount of nitrogen.

The plants with one-half their roots in the complete solution in Experiments I, II, and III absorbed, respectively, 0.77, 0.76, and 0.74 as much nitrogen as the normal plants, and absorbed, respectively, 1.45, 1.48, and 1.45 times as much nitrogen per gram of roots as the normal plants. A comparison of the results of Experiments I, II, and III with those of this experiment shows that the smaller the portion of roots supplied with nitrogen, the less nearly the plants reach the maximum absorption of



nitrogen and the greater is the amount of nitrogen absorbed per gram of roots.

EXPERIMENT V.—RICE WITH ONE-HALF THE ROOTS IN A PHOSPHORUS-FREE SOLUTION

The previous experiments yielded pretty definite figures for the relative amounts and rates of nitrogen absorption for plants partially and completely supplied with nitrogen. It was therefore of interest to see whether the same figures would hold for the absorption of other mineral elements under like conditions. In this experiment the absorption of phosphorus was tested.

The complete neutral nutrient solution was used with ferric citrate as the source of iron. The double-phosphorus solution was the same as the complete, except the quantities of both dipotassium phosphate ( $K_2HPO_4$ ) and monopotassium phosphate ( $KH_2PO_4$ ) were doubled. The no-phosphate plants were grown in 200-c. c. flasks for 40 days; all others in 200-c. c. flasks for 26 days, and in 500-c. c. flasks for 14 days. Eight flasks were taken as a unit and the units duplicated for each treatment. The solutions were changed nine times during the experiment. Experimental data are given in Tables X and XI.

TABLE X.—Growth of rice in Experiment V

| Nutrient solution.          |                             | Flask No.      | Weight of stalks and leaves. |                |                   | Number of roots. |            | Average oven-dry weight of roots. |              | Ratio of roots to tops. |
|-----------------------------|-----------------------------|----------------|------------------------------|----------------|-------------------|------------------|------------|-----------------------------------|--------------|-------------------------|
| A-flasks.                   | B-flasks.                   |                | Green.                       | Oven-dry.      | Average oven-dry. | A-flasks.        | B-flasks.  | A-flasks.                         | B-flasks.    |                         |
| Phosphorus-free             | Phosphorus-free.            | 1-8<br>9-16    | 5.03<br>6.11                 | 1.96<br>1.94   | 1.95              | 120<br>129       | 127<br>139 | 0.16<br>0.16                      | 0.74<br>0.74 | 0.666                   |
| Do.                         | Complete.                   | 17-24<br>25-32 | 192.86<br>195.01             | 30.25<br>30.25 | 30.26             | 312<br>307       | 386<br>392 | 4.80<br>4.85                      | 4.32<br>4.14 | .301                    |
| Do.                         | Complete double phosphorus. | 33-40<br>41-48 | 168.37<br>166.41             | 30.87<br>28.19 | 29.53             | 297<br>281       | 295<br>258 | 4.25<br>3.58                      | 4.14<br>3.54 | .284                    |
| Complete.                   | Complete.                   | 49-56<br>57-64 | 162.35<br>162.20             | 29.95<br>28.72 | 29.34             | 294<br>264       | 258<br>267 | 3.72<br>3.44                      | 3.54<br>3.54 | .247                    |
| Complete double phosphorus. | Complete double phosphorus. | 65-72<br>73-80 | 131.78<br>149.34             | 27.33<br>28.85 | 28.09             | 237<br>250       | 216<br>247 | 3.44<br>3.44                      | 3.54<br>3.54 | .248                    |

TABLE XI.—Phosphoric acid and nitrogen absorbed by rice in Experiment V

| Flask No. | Phosphoric acid ( $P_2O_5$ ). |                        |                             | Nitrogen (N) in dry stalks and leaves. |
|-----------|-------------------------------|------------------------|-----------------------------|--|
|           | In dry leaves and stalks.     | Absorbed by 16 plants. | Absorbed per gram of roots. |  |
|           | Per cent.                     | Gm.                    | Gm.                         | Per cent.                              |
| 1-16      | 0.17                          |                        |                             |  |
| 17-32     | 1.13                          | 0.3386                 | 0.0784                      | 4.13                                   |
| 33-48     | 1.19                          | .3481                  | .0841                       | 4.18                                   |
| 49-64     | 1.53                          | .4456                  | .0614                       | 4.43                                   |
| 65-80     | 1.53                          | .4265                  | .0611                       | 4.12                                   |

Phosphorus could not be determined accurately in roots which had grown in complete solutions, because of an adhering precipitate of ferric phosphate. Hence, in calculating the amount of phosphorus absorbed by the plants, account could be taken only of that present in the tops; the absolute figures for "grams of phosphorus pentoxid ( $P_2O_5$ ) absorbed per 16 plants" and "grams of phosphorus pentoxid ( $P_2O_5$ ) absorbed per gram of roots," in this and the following experiment, are thus considerably below the true values. The relative absorption for the different lots of plants is pretty well expressed by these figures, however, as the amount of phosphorus in the roots ought to be in fairly constant proportion to the amount in the tops, except that in plants 17 to 48 it is probably a little less than in 49 to 80, as plants 17 to 48 have some roots in the phosphorus-free solution.

If plants 49 to 64 are regarded as normal in growth and phosphorus content, it is evident that the partial-phosphorus plants, 17 to 32, made the same growth of tops as the normal plants, had 22 per cent greater ratio of roots to tops, absorbed 0.76 of the normal amount of phosphorus, and absorbed 1.28 times as much phosphorus per gram of roots as the normal plants.

Doubling the phosphates in the solution had about the same effect on the plants as doubling the nitrogen in Experiment III. When all the roots were in the complete solution, doubling the phosphates in the solution did not appreciably affect the growth of tops, the ratio of roots to tops, the amount of phosphorus absorbed, or the amount of phosphorus absorbed per gram of roots. In the case of plants with half their roots in the complete solution, doubling the phosphates in the solution had the effect of decreasing the ratio of roots to tops, very slightly increasing the amount of phosphorus absorbed, and increasing the amount of phosphorus absorbed per gram of roots.

EXPERIMENT VI.—RICE WITH TWO-THIRDS THE ROOTS IN PHOSPHORUS-FREE SOLUTION

To observe the effect of further decreasing the number of roots in the complete solution, a test was conducted in which one-third of the roots were maintained in the complete solution and two-thirds in the phosphorus-free solution.

The complete acid solution and the phosphorus-free solution were used, with ferric tartrate as the source of iron. The number of flasks per unit was the same as in the preceding test. The no-phosphate plants were grown in 200-c. c. flasks for 40 days; all others, in 200-c. c. flasks for 24 days and 500-c. c. flasks for 16 days. The solutions were changed nine times during the experiment. Experimental data are given in Tables XII and XIII.

TABLE XII.—Growth of rice in Experiment VI

| Nutrient solution. |                 | Flask No.               | Weight of stalks and leaves. |                         |                   | Number of roots.  |                   | Average oven-dry weight of roots. |                      | Ratio of roots to tops. |
|--------------------|-----------------|-------------------------|------------------------------|-------------------------|-------------------|-------------------|-------------------|-----------------------------------|----------------------|-------------------------|
| A-flasks.          | B-flasks.       |                         | Green.                       | Oven-dry.               | Average oven-dry. | A-flasks.         | B-flasks.         | A-flasks.                         | B-flasks.            |                         |
|                    |                 |                         | Gm.                          | Gm.                     | Gm.               |                   |                   | Gm.                               | Gm.                  |                         |
| Phosphorus-free    | Phosphorus-free | 1-8<br>9-16<br>17-24    | 5.53<br>5.94<br>259.07       | 1.67<br>1.75<br>39.58   | 1.71              | 128<br>152<br>595 | 144<br>155<br>265 | 0.70<br>0.70<br>7.98              | 0.76<br>0.76<br>3.86 | .865<br>.865<br>.298    |
| Do                 | Complete        | 25-32<br>33-40<br>41-48 | 260.01<br>281.28<br>284.12   | 39.94<br>38.22<br>38.50 | 39.76             | 647<br>550<br>534 | 275<br>301<br>285 | 7.98<br>6.26<br>6.26              | 3.86<br>3.28<br>3.28 | .298<br>.249<br>.249    |

TABLE XIII.—Phosphoric acid and nitrogen absorbed by rice in Experiment VI

| Flask No. | Phosphoric acid (P <sub>2</sub> O <sub>5</sub> ). |                        |                             | Nitrogen (N) in dry stalks and leaves. |
|-----------|---|------------------------|-----------------------------|--|
|           | In dry leaves and stalks.                         | Absorbed by 16 plants. | Absorbed per gram of roots. |  |
|           | Per cent.   | Gm.                    | Gm.                         | Per cent.                              |
| 1-16      |   |                        |                             | 1.49                                   |
| 17-32     | 0.87  | 0.3459                 | 0.0896                      | 3.85                                   |
| 33-48     | 1.39  | .5332                  | .0559                       | 3.92                                   |

If we assume that plants 33 to 48 were normal, 17 to 32, with one-third their roots in the complete solution, made a normal growth, had a 20 per cent higher ratio of roots to tops, absorbed 0.65 of the normal amount of phosphorus, and absorbed 1.60 times the normal amount of phosphorus per gram of roots.

Decreasing the number of roots in the complete solution had about the same effect on phosphorus absorption that it did on nitrogen absorption—that is, it decreased the total amount of phosphorus absorbed and increased the phosphorus absorbed per gram of roots. The fractions of the normal amount of phosphorus absorbed by the plants with one-half and one-third their roots in the complete solution were, respectively, 0.76 and 0.65. These figures are in good agreement with similar factors of 0.76 and 0.55 for nitrogen absorption by plants with one-half and one-fourth of their roots in the complete solution. Per gram of roots, however, the partial-phosphorus plants increased their phosphorus absorption less than the partial-nitrogen plants increased their nitrogen absorption. This was due to the fact that growths made by the partial- and complete-phosphorus plants were about equal, while the partial-nitrogen plants made less growth than the complete-nitrogen plants.

The fact that plants with only part of their roots in the complete solution made about the same growth as the normal plants, although they contained considerably less phosphoric acid, shows that the normal plants absorbed considerably more phosphorus than they needed.

It is evident that under the special conditions of these tests the absorption of phosphorus and nitrogen obey practically the same law.

EXPERIMENT VII.—RICE WITH ONE-HALF THE ROOTS IN POTASSIUM-FREE SOLUTION

It was thought that the figures for the relative absorption of potassium by plants partially and completely supplied with potassium might vary somewhat from the similar figures for nitrogen and phosphorus, since, as is well known, sodium can to a small extent replace or supplement a deficiency of potassium in the plant, while a deficiency of nitrogen or phosphorus can not be supplemented by other mineral elements.

In this experiment the complete acid solution and the potassium-free solutions shown in Table I were used, while ferric tartrate was the source of iron. Eight flasks were taken as a unit and the units duplicated for each treatment. The plants were grown for 20 days in 200-c. c. flasks and 20 days in 500-c. c. flasks. Solutions were changed 10 times during the experiment. Experimental data are shown in Tables XIV and XV.

TABLE XIV.—Growth of rice in Experiment VII

| Nutrient solution. |                    | Flask No.                                       | Weight of stalks and leaves.                                |   |   | Number of roots.                       |  | Average oven-dry weight of roots. |                      | Ratio of roots to tops. |
|--------------------|--------------------|---|---|---|---|--|--|-----------------------------------|----------------------|-------------------------|
| A-flasks.          | B-flasks.          |   | Green.  | Oven-dry.   | Average oven-dry.                       | A-flasks.                              | B-flasks.                              | A-flasks.                         | B-flasks.            |                         |
| Potassium-free.... | Potassium-free.... | 1-8<br>9-16<br>17-24<br>25-32<br>33-40<br>41-48 | Gm.<br>57.25<br>55.86<br>58.43<br>58.93<br>116.00<br>199.40 | Gm.<br>11.02<br>10.35<br>41.65<br>39.73<br>43.12<br>42.42 | Gm.<br>10.64<br>10.14<br>40.14<br>43.27 |  |  |                                   |                      |                         |
| Do.....            | Complete.....      |   |   |   |   | 225<br>220<br>438<br>417<br>504<br>514 | 252<br>247<br>467<br>449<br>498<br>499 | 1.64<br>5.47<br>4.92              | 1.84<br>5.70<br>5.51 | .187<br>.278<br>.207    |

TABLE XV.—Potash and soda absorbed by rice in Experiment VII

| Flask No. | Potash (K <sub>2</sub> O). |           |               |           |                        |                             | Soda (Na <sub>2</sub> O). |           |               |           |                       |                             |
|-----------|----------------------------|-----------|---------------|-----------|------------------------|-----------------------------|---------------------------|-----------|---------------|-----------|-----------------------|-----------------------------|
|           | In dry stalks and leaves.  |           | In dry roots. |           | Absorbed by 16 plants. | Absorbed per gram of roots. | In dry stalks and leaves. |           | In dry roots. |           | Present in 16 plants. | Absorbed per gram of roots. |
|           |                            |           | A-flasks.     | B-flasks. |                        |                             |                           |           | A-flasks.     | B-flasks. |                       |                             |
|           | Per cent.                  | Per cent. | Per cent.     | Per cent. | Gm.                    | Gm.                         | Per cent.                 | Per cent. | Per cent.     | Per cent. | Gm.                   | Gm.                         |
| 1-16      | 0.45                       | 0.43      | 0.43          | .....     | .....                  | .....                       | 1.66                      | 1.24      | 1.24          | .....     | .....                 | .....                       |
| 17-32     | 3.00                       | 1.00      | 1.35          | 1.630     | 0.288                  | .....                       | .78                       | 1.48      | 1.39          | 0.4733    | 0.0424                | .....                       |
| 33-48     | 5.25                       | 2.76      | 2.76          | 2.498     | .210                   | .....                       | .71                       | .88       | .88           | .4043     | .0354                 | .....                       |

Assuming that plants 33 to 48 were normal in growth and composition, it can be seen that the partial-potassium plants (17 to 32) had 4 per cent greater ratio of roots to tops, absorbed 0.66 of the normal amount of

potash, and absorbed 1.32 times the normal amount of potash per gram of roots. The plants partially supplied with potash absorbed considerably more soda than those completely supplied with potash. The partial-potassium plants absorbed 0.73 as much potash and soda combined as the complete-potassium plants.

EXPERIMENT VIII.—RICE WITH THREE-FOURTHS THE ROOTS IN  
POTASSIUM-FREE SOLUTION

As the figures for potash absorbed by the partial-potassium plants differed somewhat from similar figures for nitrogen and phosphorus, it was important to observe the potash absorption of plants with more roots in the potassium-free solution.

In regard to nutrient solutions, numbers of flasks per unit, and time the plants were grown in the different-sized flasks, this experiment was the same as the preceding. Solutions were changed 11 times during the experiment. Experimental data are given in Tables XVI and XVII.

TABLE XVI.—Growth of rice in Experiment VIII

| Nutrient solution. |                | Flask No.      | Weight of stalks and leaves. |                     |                   | Number of roots. |            | Average oven-dry weight of roots. |             | Ratio of roots to tops. |
|--------------------|----------------|----------------|------------------------------|---------------------|-------------------|------------------|------------|-----------------------------------|-------------|-------------------------|
| A-flasks.          | B-flasks.      |                | Green.                       | Oven-dry.           | Average oven-dry. | A-flasks.        | B-flasks.  | A-flasks.                         | B-flasks.   |                         |
| Potassium-free     | Potassium-free | 1-8<br>9-16    | Gm.<br>46.50<br>47.66        | Gm.<br>8.88<br>9.08 | Gm.<br>8.98       | 204<br>187       | 213<br>201 | Gm.<br>1.37                       | Gm.<br>1.47 | .316                    |
| Do.                | Complete       | 17-24<br>25-32 | 316.98<br>210.37             | 30.46<br>31.37      | 30.87             | 548<br>550       | 534<br>522 | 6.38                              | 2.63        | .292                    |
| Complete           | do.            | 33-40<br>41-48 | 248.06<br>249.01             | 33.86<br>34.85      | 34.31             | 572<br>579       | 568<br>579 | 6.87                              | 3.13        | .291                    |

TABLE XVII.—Potash and soda absorbed by rice in Experiment VIII

| Flask No. | Potash (K <sub>2</sub> O). |           |           |                       |                             | Soda (Na <sub>2</sub> O). |           |           |                       |                             |
|-----------|----------------------------|-----------|-----------|-----------------------|-----------------------------|---------------------------|-----------|-----------|-----------------------|-----------------------------|
|           | In dry roots.              |           |           |                       | Absorbed per gram of roots. | In dry roots.             |           |           |                       | Absorbed per gram of roots. |
|           | In dry stalks and leaves.  | A-flasks. | B-flasks. | Present in 16 plants. |                             | In dry stalks and leaves. | A-flasks. | B-flasks. | Present in 16 plants. |                             |
|           | Per cent.                  | Per cent. | Per cent. | Gm.                   | Gm.                         | Per cent.                 | Per cent. | Per cent. | Gm.                   | Gm.                         |
| 1-16      | 0.47                       | 0.33      | 0.33      | 1.62                  | 1.12                        | 1.12                      | 1.12      | 1.12      | 0.3473                | 0.0386                      |
| 17-32     | 4.15                       | 1.06      | 1.95      | 1.3482                | 0.515                       | .72                       | 1.55      | 1.00      | 0.3473                | 0.0386                      |
| 33-48     | 5.76                       | 2.76      | 2.76      | 2.2018                | .220                        | .35                       | .65       | .65       | .1851                 | .0185                       |

Compared with the complete-potassium plants, the partial-potassium plants made slightly less growth, had the same ratio of roots to tops, absorbed 0.61 as much potassium, and absorbed 2.34 times as much potassium per gram of roots. The fact that partial-potassium plants

absorbed, with 29 per cent of their roots, 0.61 as much potassium as the complete plants is in good agreement with the results for nitrogen and phosphorus, where, with 27 per cent and 33 per cent of the roots, the absorptions were, respectively, 0.55 and 0.65.

In this and the preceding experiment the plants partially supplied with potassium absorbed considerably more sodium than plants completely supplied with potassium.

EXPERIMENT IX.—RICE WITH ONE-HALF THE ROOTS IN AN IRON-FREE SOLUTION (FERROUS SULPHATE SOURCE OF IRON)

As nitrogen, phosphorus, and potash are similar in being used by plants in relatively large amount, it was important to test the absorption of a mineral element used by the plant in small amount. Iron was used in this test, as this element is present in most plants in relatively minute quantities and as a deficiency markedly affects growth.

In this test approximately half the roots of the partial-iron plants were maintained in the iron-free solution. Both acid and neutral nutrient solutions were used. Ferrous sulphate was the source of iron, used so as to supply 0.008 gm. of iron per liter during the first 10 days of the test, 0.004 gm. of iron per liter during the next 10 days, and 0.002 gm. of iron per liter during the last 20 days. Four flasks were taken as a unit and the units triplicated for each treatment. The no-iron plants were grown in 200-c. c. flasks for 40 days; all others in 200-c. c. flasks for 27 days, and 500-c. c. flasks for 13 days. Solutions were changed six times during the experiment. Experimental data are given in Tables XVIII and XIX.

TABLE XVIII.—Growth of rice in Experiment IX

| Nutrient solution. |                  | Flask No. | Weight of stalks and leaves. |           |                   | Average oven-dry weight of roots. |           |       | Ratio of roots to tops. |
|--------------------|------------------|-----------|------------------------------|-----------|-------------------|-----------------------------------|-----------|-------|-------------------------|
| A-flasks.          | B-flasks.        |           | Green.                       | Oven-dry. | Average oven-dry. | A-flasks.                         | B-flasks. |       |                         |
|                    |                  |           | Gm.                          | Gm.       | Gm.               | Gm.                               | Gm.       |       |                         |
| Iron-free neutral  | Iron-free acid   | 1-4       | 1.42                         | 0.26      |                   |                                   |           |       |                         |
|                    |                  | 5-8       | 1.39                         | .26       | 0.26              | 0.057                             | 0.041     | 0.377 |                         |
|                    |                  | 9-12      | 1.37                         | .26       |                   |                                   |           |       |                         |
|                    |                  | 13-16     | 29.62                        | 4.10      |                   |                                   |           |       |                         |
| Complete neutral   | do               | 17-20     | 33.86                        | 4.78      | 4.38              | .632                              | .547      | .269  |                         |
|                    |                  | 21-24     | 31.19                        | 4.27      |                   |                                   |           |       |                         |
|                    |                  | 25-28     | 49.25                        | 6.34      |                   |                                   |           |       |                         |
|                    |                  | 29-32     | 53.67                        | 7.03      | 6.61              | .989                              | .772      | .266  |                         |
| Do                 | Complete neutral | 33-36     | 50.49                        | 6.48      |                   |                                   |           |       |                         |
|                    |                  | 37-40     | 36.16                        | 4.78      |                   |                                   |           |       |                         |
| Iron-free neutral  | Complete acid    | 41-44     | 38.55                        | 5.09      | 4.60              | .539                              | .722      | .274  |                         |
|                    |                  | 45-48     | 26.85                        | 3.93      |                   |                                   |           |       |                         |
|                    |                  | 49-52     | 48.42                        | 5.99      |                   |                                   |           |       |                         |
|                    |                  | 53-56     | 48.76                        | 6.22      | 6.27              | .902                              | .984      | .301  |                         |
| Complete acid      | do               | 57-60     | 51.97                        | 6.61      |                   |                                   |           |       |                         |

TABLE XIX.—*Iron and nitrogen absorbed by rice in Experiment IX*

| Flask No. | Iron (FeO <sub>2</sub> )  |                       |                             | Nitrogen (N) in dry stalks and leaves. |
|-----------|---------------------------|-----------------------|-----------------------------|--|
|           | In dry stalks and leaves. | Absorbed by 8 plants. | Absorbed per gram of roots. |  |
|           | Per cent.                 | Gm.                   | Gm.                         | Per cent.                              |
| 1-12      | 0.0400                    |                       |                             | 3.90                                   |
| 13-24     | .0229                     | 0.000899              | 0.00142                     | 3.90                                   |
| 25-36     | .0223                     | .001370               | .00078                      | 3.80                                   |
| 37-48     | .0378                     | .001635               | .00227                      | 3.72                                   |
| 49-60     | .0378                     | .002266               | .00120                      | 3.70                                   |

This was one of the preliminary experiments conducted in a study of the assimilation of iron by rice from certain nutrient solutions (5). It was found that ferrous sulphate, used at this diminishing rate of 0.008, 0.004, and 0.002 gm. of iron per liter, apparently did not furnish sufficient available iron for an optimum growth of the plants. Because of this insufficiency of iron it was to be expected that plants with half their roots in the complete solution would absorb only half as much iron as those with all their roots in the complete solution, the former having only half as much iron at their disposal as the latter. This would doubtless have been the case if the available iron had been a fixed quantity in the solution. Other work showed, however, that most of the iron was not present in true solution, that the quantity of iron available was probably dependent on the rate at which iron went into solution, and that this rate was influenced by the rate at which it was removed by the plant. As plants with only half their roots in the complete solution would absorb iron more quickly than plants with all their roots, they might absorb more than half the quantity of iron.

If plants 13 to 24 are compared with 25 to 36, where the iron was added to the neutral nutrient solution, it can be seen that the partial-iron plants absorbed 0.66 as much iron as the complete-iron plants and absorbed 1.82 times as much per gram of roots. If we compare plants 37 to 48 with 49 to 60, where the iron was added to the acid nutrient solution, it can be seen that the partial-iron plants absorbed 0.72 as much iron as the complete-iron plants and absorbed 1.89 times as much iron per gram of roots.<sup>1</sup> The ratio of roots to tops varied little between the partial- and complete-iron plants in either the acid or the neutral solution. The figures for the relative amounts of iron absorbed by the partial- and complete-iron plants agree fairly well with similar figures for the other nutrients.<sup>2</sup>

<sup>1</sup> Small amounts of iron from ferrous sulphate are more available in the acid than in the neutral solution.

<sup>2</sup> There is another source of doubt in this experiment aside from the insufficiency of iron referred to above. Both ferrous and ferric iron were doubtless present in the solutions, and the plants probably absorbed both forms of iron. It is pointed out in another place (5) that there may be a difference in the efficiency of these two forms of iron in the plant. At all events, in several experiments ferrous sulphate was a less efficient form of iron than ferric compounds. The much higher percentage of iron in the plants grown in the acid solution is probably due to a greater absorption of ferrous iron.

EXPERIMENT X.—RICE WITH HALF THE ROOTS IN AN IRON-FREE SOLUTION (FERRIC TARTRATE SOURCE OF IRON)

The results of the previous experiment were not decisive, as there was a strong probability that neither the complete- nor the partial-iron plants had a sufficiency of iron available in the solution. Previous work showed, however, that in the acid solution with 0.008 gm. of iron per liter from ferric tartrate, plenty of iron was available; in fact, rice absorbed a certain excess of iron from this solution. Accordingly a test was run, using the acid solution with ferric tartrate.

In this test no plants were grown without iron, as the previous test and many others (5) showed that the growth of such plants was practically nil. Therefore, it would not appreciably affect the figure for the relative amounts of iron absorbed by partial- and complete-iron plants whether the quantity of iron in the no-iron plants was subtracted or not. The plants were grown 24 days in 200-c. c. flasks and 16 days in 500-c. c. flasks. Seven flasks were taken as a unit and the units duplicated for each treatment. Solutions were changed 10 times during the experiment. The results are given in Tables XX and XXI.

TABLE XX.—Growth of rice in Experiment X

| Nutrient solution. |               | Flask No.      | Weight of stalks and leaves. |              |                   | Number of roots. |            | Average oven-dry weight of roots. |             | Ratio of roots to tops. |
|--------------------|---------------|----------------|------------------------------|--------------|-------------------|------------------|------------|-----------------------------------|-------------|-------------------------|
| A-flasks.          | B-flasks.     |                | Green.                       | Oven-dry.    | Average oven-dry. | A-flasks.        | B-flasks.  | A-flasks.                         | B-flasks.   |                         |
| Iron-free.....     | Complete..... | 1-7<br>8-14    | Gm.<br>266.5                 | Gm.<br>277.1 | Gm.<br>38.79      | 324<br>283       | 379<br>264 | Gm.<br>4.23                       | Gm.<br>5.18 | 0.245                   |
| Complete.....      | do.....       | 15-21<br>22-28 | Gm.<br>304.3                 | Gm.<br>326.8 | Gm.<br>45.01      | 358<br>396       | 378<br>403 | Gm.<br>5.53                       | Gm.<br>5.95 | .213                    |

TABLE XXI.—Iron, nitrogen, and phosphoric acid absorbed by rice in Experiment X

| Flask No. | Iron (Fe <sub>2</sub> O <sub>3</sub> ). |                        |                             | Nitrogen (N) in dry stalks and leaves. | Phosphoric acid (P <sub>2</sub> O <sub>5</sub> ) in dry stalks and leaves. |
|-----------|---|------------------------|-----------------------------|--|--|
|           | In dry stalks and leaves.               | Absorbed by 14 plants. | Absorbed per gram of roots. |  |  |
| 1-14      | Per cent.<br>0.0189                     | Gm.<br>0.00733         | Gm.<br>0.00136              | Per cent.<br>3.64                      | Per cent.<br>1.34  |
| 15-28     | 0.0246                                  | 0.01107                | 0.00096                     | 3.53                                   | 1.33   |

Comparison with the complete-iron plants (15 to 28) shows that the partial-iron plants (1 to 14) absorbed 0.66 as much iron and 1.43 times as much iron per gram of roots. The ratio of roots to tops and the percentages of nitrogen and phosphoric acid in the dry substance varied little between the two lots of plants



## SUMMARY OF EXPERIMENTAL RESULTS

The essential results of the 10 preceding experiments are summarized in Table XXII.

TABLE XXII.—Summary of results of Experiments I to X

| Experiment No. | Plant grown. | Element tested. | Complete nutrient solution. | Proportion of roots in complete solution. | Total amount of element absorbed. | Amount of element absorbed per gram of roots. <sup>a</sup> | Ratio of root to top. <sup>a</sup> |
|----------------|--------------|-----------------|-----------------------------|---|-----------------------------------|--|------------------------------------|
| I.....         | Rice.....    | Nitrogen.....   | Neutral.....                | <i>Per ct.</i>                            |                                   |  |                                    |
| II.....        | Corn.....    | do.....         | do.....                     | 50  | 77                                | 145  | 123                                |
| III.....       | Rice.....    | do.....         | do.....                     | 56  | 76                                | 145  | 123                                |
| III.....       | do.....      | do.....         | Neutral, double nitrogen.   | 54  | 74                                | 125  | 122                                |
| III.....       | do.....      | do.....         | do.....                     | 54  | 77                                | 162  | 113                                |
| IV.....        | do.....      | do.....         | Neutral.....                | 27  | 55                                | 226  | 133                                |
| V.....         | do.....      | Phosphorus..... | do.....                     | 47  | 76                                | 128  | 122                                |
| V.....         | do.....      | do.....         | Neutral, double phosphorus. | 50  | 78                                | 137  | 115                                |
| VI.....        | do.....      | do.....         | Neutral.....                | 33  | 65                                | 160  | 126                                |
| VII.....       | do.....      | Potassium.....  | Acid.....                   | 31  | 66                                | 132  | 104                                |
| VIII.....      | do.....      | do.....         | do.....                     | 39  | 61                                | 154  | 100                                |
| IX.....        | do.....      | Iron.....       | Neutral, ferrous sulphate.  | 54  | 66                                | 122  | 102                                |
| IX.....        | do.....      | do.....         | Acid, ferrous sulphate.     | 57  | 72                                | 129  | 97                                 |
| X.....         | do.....      | do.....         | Acid, ferric tartrate.      | 56  | 66                                | 143  | 97                                 |

<sup>a</sup> Total amount of element absorbed, amount absorbed per gram of roots, and root to top ratio, each taken as 100 for plants with all roots in the complete solution. Corresponding values for plants with part of roots in complete solution expressed relative to 100.

The amount of nitrogen or phosphorus absorbed by plants with half their roots in the complete solution was 0.76 of that absorbed by plants with all their roots in the complete solution, while the similar figure for potassium and iron was 0.66. As already pointed out, it was to be expected that a somewhat different figure would be obtained for potassium than for nitrogen and phosphorus, as a lack of potassium can be supplemented to some extent by an abundance of sodium. The lower figure for iron may be connected with the immobility of iron in the plant (4).

The less absorption of an element supplied to only part of the roots of a plant was not due to the partial plants having a smaller absolute amount of the element available than the complete plants. This was proved by the results of Experiments III and V, where doubling the quantity of nitrogen or phosphorus in the solution supplied to half the roots did not appreciably increase the amounts of nitrogen or phosphorus absorbed by these plants.

It is apparent that the fewer roots in the complete solution the less nearly the plants reached the optimum absorption. The decrease from the optimum absorption was not, however, directly proportional to the portion of roots in the complete solution. The relation between the portion of roots in the complete solution and the fraction of the maximum amount of nitrogen absorbed is shown by the curve in figure 1.

The maximum amount of nitrogen, 100, is taken as that absorbed by plants with 100 per cent of their roots in the complete solution. As plants with no roots in a complete solution (the incomplete solution being nitrogen-free) can absorb no nitrogen, the zero point is also fixed. The two other points found experimentally for plants with 27 per cent and 53 per cent of their roots<sup>1</sup> in the complete solution determine fairly well the form of the curve.

From the uniformity of the preceding results it seems permissible to state, as a rule, that when all the roots of a plant are supplied with all the essential elements except one, the fewer the roots supplied with the one lacking element the less nearly the plant will attain a maximum absorption of this element. As this rule has been found valid for nitrogen, phosphorus, potassium, and iron, it probably applies to all the mineral nutrients. The rule holds when the total quantity of the element supplied is equal to or in excess of the needs of the plant. If the total quantity of element supplied is insufficient for the needs of the

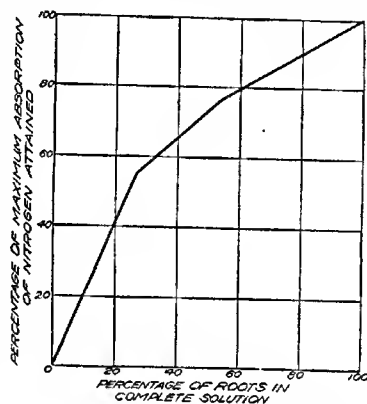


FIG. 1.—Relation between portion of roots supplied with nitrogen and portion of maximum absorption attained.

plant, a more equal absorption of the element by plants with part and with all their roots might be expected. This, however, has not been proved.

The relative amounts of the element absorbed per gram of roots by plants with part and with all their roots supplied with the element varied considerably, according to several conditions, although this figure was always much higher for the plants partially supplied than for those completely supplied. The greater the depression of growth by the smaller total amount of the element absorbed by the plants partially supplied, the greater was the quantity of the element absorbed per gram of roots. When the partially supplied plants had a greater ratio of roots to tops than the completely supplied plants, the absorption per gram of roots for the partial plants did not so greatly exceed that of the complete plants. The smaller the portion of roots in the complete solution, the greater was the absorption of the element per gram of roots in the complete solution.

<sup>1</sup> The average of results from Experiments I to IV are used.

It was expected that plants whose growth was restricted by having a portion of the roots present in the incomplete solution would show an increased absorption of elements present in both the incomplete and complete solutions. The results did not justify the expectation, except in the case of plants partially supplied with potassium. In Experiments I, II, III, and IV the partial-nitrogen plants contained practically the same percentages of phosphoric acid as plants completely supplied with nitrogen. In Experiments V and VI the partial-phosphorous plants contained about the same percentages of nitrogen as the complete-phosphorous plants. In Experiments VII and VIII the partial-potassium plants contained considerably more sodium than the complete-potassium plants. And in Experiments IX and X the partial-iron plants contained practically the same percentages of nitrogen and phosphoric acid as the complete-iron plants.

It will be noted that, in all the experiments with nitrogen or phosphorus, plants with part of their roots in the complete solution had a considerably greater ratio of roots to tops than plants with all their roots in the complete solution. It might be thought that this was due to the incomplete solution furnishing a better medium for growth, aside from nutritive effects, than the complete solution. A calculation of the average weights of individual roots in the two solutions shows this assumption to be incorrect and suggests that the increased ratio of roots to tops of the partial plants was due to an adaptation of the plant under the stimulus of a deficiency of the element. The calculations show that, with plants partially supplied with nitrogen or phosphorus, the average weight of roots in the nitrogen- or phosphorus-free solution was slightly less in nearly every case than the weight of roots in the complete solution. Also the average weight of roots in the complete solution of plants with part of their roots in the complete solution was slightly greater than the weight of roots of plants with all their roots in the complete solution.

In experiments where potash or iron was the lacking element the plants with part of their roots in the complete solution did not have an appreciably different ratio of roots to tops from plants with all their roots in the complete solution. This was probably due to the fact that rice does not so readily respond, by greater root growth, to a certain deficiency of these elements. As the plants receiving absolutely no potassium or iron had a markedly increased ratio of roots to tops, it is apparent that the difference in the response to a lack of nitrogen and phosphorus or potassium and iron is chiefly one of degree.

#### DISCUSSION OF RESULTS

The two chief facts brought out in the preceding cultural tests are (1) that the fewer roots supplied with an ion the greater is the absorption of the ion per gram of roots, and (2) that a plant is unable to attain a

maximum absorption by means of only a portion of its roots. It is not felt that a fully adequate explanation can be given of these facts until more is known of the mechanism and dynamics of absorption, translocation, and utilization of mineral elements in the plant. The following explanation is offered, not as an hypothesis, but more as a suggestion of the general way in which the results may have been brought about.

Roughly it may be said that the absorption of a mineral element is dependent on utilization, that, as the ions are removed by formation of new compounds, etc., in the plant, more ions can be absorbed. Under the special conditions of the tests described here, absorption is primarily dependent on utilization, but the rate at which ions can be translocated from the absorbing cells to the utilizing cells also affects both utilization and absorption.<sup>4</sup> When one-half the roots of a plant are supplied with an ion, it may be said that the plant absorbs only three-fourths as much of the ion as when all the roots are supplied, because the rate of transference from the absorbing cells to the utilizing cells is diminished by one-fourth. The transference of ions from the cells where they are absorbed to the cells where they are utilized, of course, involves a series of translocations. In speaking, as is done above, of the rate of transference from absorbing to utilizing cell, the average rate of the whole series of translocations is understood.

While the total amount of an ion absorbed by a plant would thus be partially dependent on the rate at which the whole series of transferences from absorbing to utilizing cells proceeded, the quantity of an ion absorbed per gram of roots would depend, not on the rate of the whole series of translocations, but on the rate of translocation from the root cells. It can be supposed that the fewer the roots supplied with an ion, the faster will the translocation of the ion from the absorbing and root cells proceed, but the slower will be the rate of the whole series of translocations. Thus, when a portion of the roots are supplied with an ion, the amount absorbed per gram of roots may be greater and the total absorbed may be less than when all the roots of a plant are supplied with an ion. This is illustrated in figure 2.

In this figure *DE* represents the rate of transference in the plant when one-fourth the roots are supplied with an ion, and *AB* the rate when all the roots are supplied. The rate of transference at *O*, the absorbing cells, are respectively *DO* and *AO*, *DO* being 2.26 times *AO*. The average rates of the whole curves are  $\frac{ODEC}{OC}$  and  $\frac{OABC}{OC}$ , the former being 0.55 of the latter.

As the conditions of the preceding experiments were ideal in the sense that there were sufficient available mineral nutrients at all times, the results were due to the way the plant functions in absorbing mineral elements. The results are, therefore, to a certain extent applicable to soil conditions and have a direct practical bearing.

<sup>4</sup> Utilization and absorption are, of course, reciprocally dependent.

It is obviously important to apply fertilizers in such a way that, so far as possible, all the roots of the plants will be supplied with the fertilizing element. The lateral diffusion of fertilizer salts in the soil being small, this can best be done by distributing the fertilizer uniformly over the whole area occupied by the roots. Whether a field plant will, with a portion of its roots, absorb all the fertilizing element applied depends on whether the quantity applied is sufficient for the needs of the plant and on various actions taking place in the soil, as leaching, fixation, etc. This work shows, however, that the optimum condition will be obtained by applying the fertilizer to all the roots. While the plant shows a degree of adaptation in its absorption as shown in these tests, it is not safe to assume that it will capture all the fertilizer wherever applied.

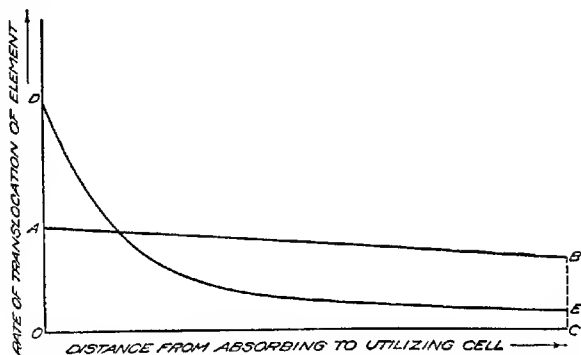


FIG. 2.—Possible relative rates of translocation of an element in plants with one-fourth and all their roots supplied with the element.

In the preceding work it was not shown whether a plant can absorb a maximum amount of an element when it is available to a certain fraction of all the roots, as the lower, upper, middle, or different parts of all the roots. It is to be expected, however, that the results obtained in this work would apply equally to this similar condition. If the idea is carried a step farther, it would also be expected that a maximum absorption would be attained only when all the absorbing cells of a root were supplied with the nutrient.

If the latter assumption is correct, a maximum absorption of the mineral nutrients from the soil would depend on all the nutrients being available throughout the soil. Since the plant for the most part obtains its nutrients from the aqueous film surrounding the soil particles, a theoretically maximum absorption would be obtained only when all the essential elements were present in all the soil films with which the roots came in contact. While this is plainly carrying the results actually

obtained pretty far afield, some of these assumptions appear to be substantiated by other work, the results of which it is hoped to present later.

The results of the preceding work have some bearing on the law of minimum. The curve in figure 1, showing the percentage of the maximum absorption of nitrogen attained when different percentages of the roots are supplied with nitrogen, has a form similar to that which Mitscherlich claims for the minimum curve (7, 8). The formula deduced by Mitscherlich for the way in which plant growth increases with increase of the minimum factor is—

$$\log. (A-y) = \log. (A-a) - K \cdot x.$$

$x$  is the vegetative factor present in minimum. In our case it is the percentage of roots in the complete solution.

$y$  is the yield obtained for any value of  $x$ . In our case it is the total amount of the element absorbed by the plants with any portion of the roots in the complete solution. The amount of the element absorbed is expressed relative to 100, as in Table XXII.

$A$  is the maximum yield obtainable, under the conditions, by increase of  $x$ . In our case  $A$  will be the absorption attained when 100 per cent of the roots are in the complete solution. This is taken as 100 in each experiment.

$a$  is the yield obtaining without any addition of  $x$ . In our case  $a$  is obviously always 0, as there can be no absorption of the element when no roots are supplied.

$K$  is a constant, "the differential factor."

By the substitution of the values obtained in Experiment I, as shown in Table XXII, the equation would be—

$$\log. (100-77) = \log. (100-0) - K \cdot 50$$

$$K = 0.0128$$

By the use of the data of experiments on the absorption of nitrogen and phosphorus afforded by Experiments I to VI in Table XXII, the following values for  $K$  were obtained:<sup>1</sup>

0.0128  
.0111  
.0108  
.0118  
.0128  
.0128  
.0132  
.0138

Average value, 0.0124— $\pm$  0.0003

<sup>1</sup> The values for the absorption of potash were not used on account of the probable partial replacement of potash by soda. Using the data for iron absorption in Experiments IX and X, the values for  $K$  are, respectively, 0.0087, 0.0091, and 0.0084, average 0.0089. The fact that a different value for  $K$  was obtained in the experiments on iron absorption does not mean that the formula fails to hold here, but merely expresses the difference, already noted, between the absorption of iron and nitrogen or phosphorus.

The value for  $K$  is sufficiently constant to create a strong probability that Mitscherlich's mathematical expression (7) represents the relation between the quantity of roots supplied with an element and the amount absorbed. The results may therefore be taken as further proof that Mitscherlich's formulation of the law of minimum is correct for ideal conditions.

#### SUMMARY

Tests were conducted in water cultures to see whether a plant could absorb a maximum amount of one mineral element which was supplied to only part of the roots if all other essential elements were supplied to all the roots. The absorption of nitrogen with rice and corn and of phosphorus, potassium, and iron with rice was tested in this way, one-half the roots being maintained in a nutrient solution lacking one of these elements. Tests were also conducted, varying the portion of roots in the complete and incomplete solutions.

The results show that, under the conditions described, the plant does not absorb a maximum amount of the element, and the fewer the roots supplied with the element, the smaller the total amount absorbed. This applies when the total amount of the element supplied is equal to or in excess of the needs of the plant. A curve was plotted showing approximately what portion of the maximum absorption can be expected with any fraction of the roots supplied with the element. With nitrogen and phosphorus the total amount absorbed by plants with half their roots in the complete solution was 0.76 of that absorbed by plants with all their roots in the complete solution. The similar figure for potassium or iron was 0.66. Increasing the concentration of the element in question in the complete solution did not appreciably alter the results.

The amount of the element absorbed per gram of roots increased greatly as the number of roots in the complete solution was diminished.

The results are explained on the basis of the rate of utilization and transference of the elements in the plant.

Attention is called to the bearing of these results on the method of applying fertilizers.

The results obtained agree with Mitscherlich's formulation of the law of minimum.

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